

## LITERATURE CITED

- BRECKON, G. J. and M. G. BARBOUR. 1974. Review of North American Pacific Coast beach vegetation. *Madroño* 22:333-360.
- DURRENBERGER, R. W. 1965. Patterns on the land. National Press Books, Palo Alto, Calif.
- HOWELL, J. T. 1957. The California flora and its province. *Leaf. W. Bot.* 8:133-138.
- RUSSELL, R. J. 1926. Climates of California. *Univ. Calif. Publ. Geogr.* 2:73-84.
- STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35:1-35.
- THORNWAITE, C. W. 1941. USDA Atlas of climatic types of the United States, 1900-1939. Misc. Publ. No. 421, U.S. Govt. Printing Office.
- VAN DYKE, E. C. 1919. The distribution of insects in western North America. *Ann. Entomol. Soc. Amer.* 12:1-12.
- . 1929. The influence which geographical distribution has on the production of the insect fauna of North America. 4th Intern. Congr. Entom. Proc., pp. 556-566.

SYNTHETIC HYBRIDIZATION AND TAXONOMY OF  
WESTERN NORTH AMERICAN *DICHANTHELIUM*,  
GROUP LANUGINOSA (POACEAE)

RICHARD SPELLENBERG

Department of Biology, New Mexico State University, Las Cruces 88003

*Dichanthelium* has been recognized to differ from the bulk of *Panicum* since 1910 when Hitchcock and Chase described it as a subgenus containing nearly 120 species. Recently elevated to generic rank (Gould, 1974), it differs from *Panicum* by morphological, anatomical, and cytological characters, and by having a  $C_3$ , rather than a  $C_4$ , photosynthetic pathway (Clark and Gould, in press). In contrast to the widespread pantropical and warm temperate *Panicum*, *Dichanthelium* occurs in a geographically limited area, being mostly North American, a few species ranging into the West Indies and to northern South America. Whether it is a recent or ancient derivative from basic panicoid stock presently cannot be ascertained. However, the several kinds of differences between one genus and the other, although each difference alone is possibly not of significance for generic segregation, when taken together indicate natural phyletic units. Even though only a small morphological gap separates *Dichanthelium* from *Panicum*, the segregation can be justified since the two resultant genera are natural and remain large, meeting the recommendation of the inverse ratio between the size of genera and their intervening gap (summarized by Mayr, 1968, pp. 234-238).

The early part of this paper uses *Panicum* nomenclature rather than that of *Dichanthelium* since literature using the former is so widely available. The dichanthelium panicums are notorious for the taxonomic difficulties that arise when one attempts to delimit species, and as a result taxonomic treatments vary from extreme "splitting" to extensive "lumping" (Shinners, 1944). Within subg. *Dichanthelium*, Hitchcock and Chase (1910) aggregated the numerous species into 17 taxonomically informal groups. One of these, group Lanuginosa, has only three common, traditionally recognized species in western United States, *P. occidentale* Scribn., *P. pacificum* Hitchc. & Chase, and *P. thermale* Bol. (Hitchcock, 1951; Hitchcock and Chase, 1910). These three species plus a fourth in the group Oligosanthos, *P. scribnerianum* Nash, present a much simpler situation in the West than in eastern United States where the bulk of the species occur; however, the patterns of variation seen in the West and the kinds of taxonomic problems evident, although less complex, seem to mirror those of eastern members of the genus. Lelong (1965) and Spellenberg (1975) have demonstrated that at least part of the taxonomic problems with these grasses results from a high incidence of autogamy combined with occasional successful outbreeding.

Early taxonomists generally applied to the western forms names now used for eastern species (cf. Spellenberg, 1968, for a complete review). Among the most commonly used was *Panicum dichotomum* L., considered by Watson (1880), Vasey (1885), and Jepson (1911) to refer to a variable species. *Panicum pubescens* Lam. or Michx. is also a name applied to most of the species in the Lanuginosa group at one time or another (Hitchcock and Chase, 1910). From about 1860 to 1910 several of the western Lanuginosa forms were described as species separate from eastern ones, and four of these, *P. thermale*, *P. occidentale*, *P. shastense* Scribn. & Merr., and *P. pacificum*, were recognized by Hitchcock and Chase (1910). They also reported the eastern species *P. huachucae* Ashe and *P. tennesseense* Ashe to have a few outlying populations in Colorado, Utah, and Arizona.

*Panicum thermale*, *P. pacificum*, and *P. occidentale*, as recognized by Hitchcock and Chase (1910) and Hitchcock (1951), were said to differ mainly by vestiture, particularly that of the adaxial surfaces of the blades. *Panicum thermale* is "velvety-villous", *P. pacificum* is "pilose", and *P. occidentale* (especially the blades) is nearly glabrous (Hitchcock, 1951). The nature of the pubescence does not change when plants are brought from the field and grown under uniform greenhouse conditions, removing the possibility that the quality and quantity of pubescence respond directly to ecological conditions. The intergradation between these forms and variation in the habit of plants, a feature also used to distinguish *P. pacificum* from *P. occidentale*, are discussed in the taxonomic section. The species show virtually no geographic separation (fig. 1), and the stated ecological differences recorded in the literature

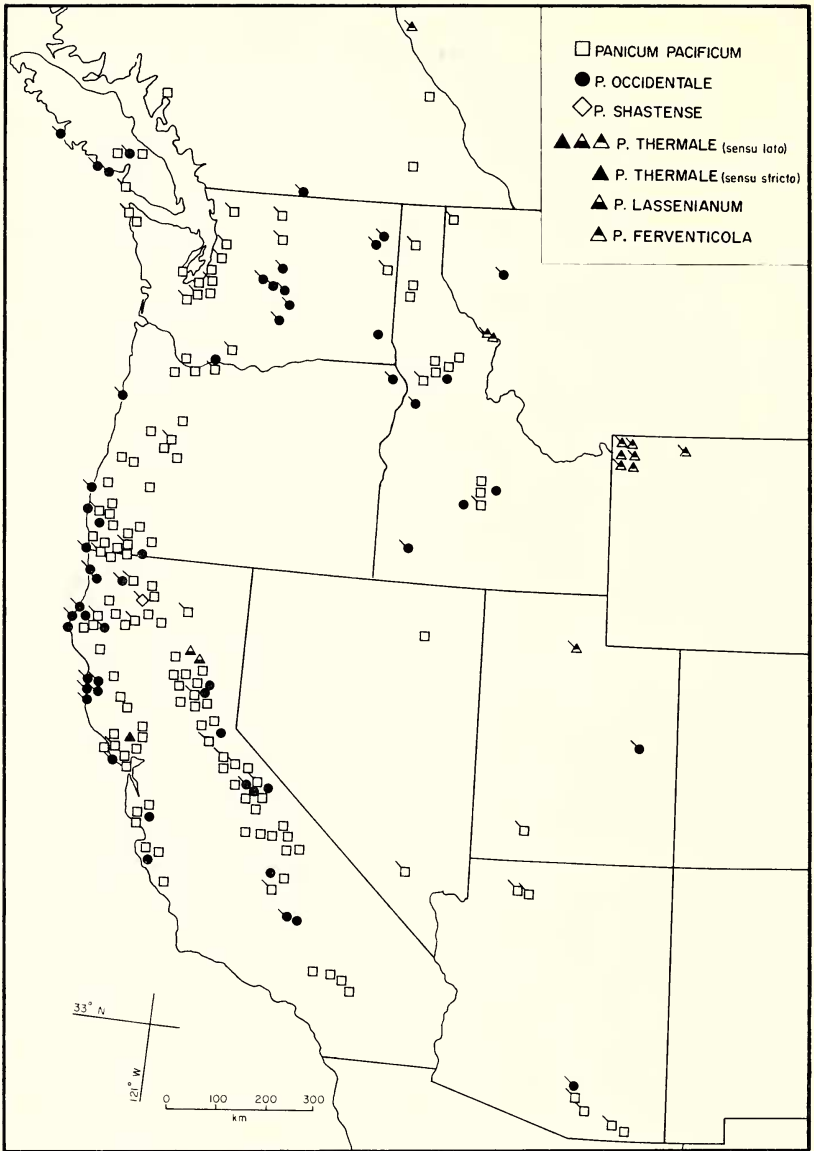


FIG. 1. Distribution of *Panicum*, group Lanuginosa in western North America, following nomenclature of earlier classifications. Rays on the upper left of some figures represent plants with the largest spikelets less than 1.8 mm long.

are non-existent when the species are examined over their entire ranges.

Although Hitchcock and Chase's treatment (1910) was followed in most western floristic works for the next 60 years, a few authors chose to recognize fewer species. Fernald (1921), noting intergradation be-

tween the members of the eastern portion of the complex, included *P. pacificum* in an enlarged and variable *P. lindheimeri* Nash. In 1934, he included this under *P. lanuginosum*, broadening the species even further. Floristic treatments using similarly broad and inclusive species concepts have been produced for the eastern United States (e.g., Gleason, 1952; Pohl, 1947). Spellenberg (1969) indicated that the western forms might not be separable from eastern species but maintained all those from the West under the oldest northwestern name, *P. occidentale*, excluding the population of *P. thermale* from Sonoma Co., California. Schmoll (1939), in her study of *Panicum thermale*, chose to recognize more species in the West than those recognized by Hitchcock and Chase. She noted that plants from (1) The Geysers, Sonoma Co., California, (2) Lassen Volcanic National Park, California, and (3) Yellowstone National Park, Wyoming, and Banff, Alberta, formed three more or less distinct groups, which she named *P. thermale*, *P. lassenianum*, and *P. ferventicola*, respectively. Her treatment reflects the morphological differences between populations previously regarded as one species and certainly obviates the problem of how *P. thermale* (sensu lato) attained such a geographic distribution (fig. 1). However, the recognition of these populations each at the specific level seems artificial when one considers the numerous intergrading forms occurring in the closely related species, *P. pacificum* and *P. occidentale*, from nearby, non-hydrothermal areas.

In attempting to separate western species from closely related eastern ones, especially *P. huachucae*, *P. tennesseense*, and *P. lanuginosum* Ell., Hitchcock and Chase (1910) used such features as the autumnal habit (due primarily to the extent and region of branching on the culms), quality and quantity of pubescence, and spikelet length. However, even a cursory examination of plants in the field and of herbarium specimens indicates that the vegetative features mentioned are variable and will not serve alone or in combination to separate species. There is a tendency then to rely on the easily measurable length of the spikelets. *Panicum huachucae* and *P. tennesseense* have spikelets 1.6–1.8 mm long, whereas *P. occidentale* and *P. pacificum* have spikelets 1.8–2.0 mm long. Plants of the eastern species rarely have spikelets exceeding the range stated, but western plants commonly have the largest spikelets less than 1.8 mm long (fig. 1), a fact that has been consistently overlooked. They would be identified as eastern species if the geographic origin of the collection were not known.

As numerous authors of eastern floras have noted, *P. huachucae* intergrades with the southeastern United States *P. lanuginosum* and there is an increasing tendency to use the latter name for all these closely related forms. *Panicum huachucae* differs somewhat in its more erect habit and by its "short-pilose" adaxial blade surfaces, whereas *P. lanuginosum* is "velvety-villous" (Hitchcock, 1951), but in eastern Texas and for some collections from the Southeast the distinction is moot.

In an attempt to understand the possible interrelationships among the western populations of these grasses and also between eastern and western species, a series of synthetic hybridizations was made. These are reported below. Chromosome numbers are reported in Table 1, and morphological characteristics are discussed in the taxonomic section. Additional chromosome counts, a study of phenolic compounds (not identified) by paper chromatography, and studies of leaf anatomy were also made, but none of these techniques (fully reported in Spellenberg, 1968) produced a means of differentiating between the western species as traditionally recognized.

TABLE 1. GEOGRAPHIC ORIGIN, CHROMOSOME NUMBER, AND SPECIMEN VOUCHERS OF *DICHANTHELIUM* USED IN HYBRIDIZATION EXPERIMENTS IN THIS STUDY. *Panicum* nomenclature of Hitchcock, 1951, is followed for ease in comparison to Figures 2 and 3. Collection numbers are the author's unless otherwise noted. Vouchers are deposited at WTU, partial sets at NY and NMC.

---

*P. huachucae*,  $n = 9$

New York, Bronx, New York Botanical Garden, rock outcrop. progeny grown from seed from 2158.

*P. lanuginosum*,  $n = 9$

Alabama, Baldwin Co., 3 mi SW of Bay Minette on U. S. Highway 31, in woods, progeny grown from seed from 1862.

*P. lindheimeri*,  $n = 9$ .

Texas, Brazos Co., 2 mi E of College Station, *F. W. Gould 11957*.

*P. occidentale*,  $n = 9$

Idaho, Custer Co., 10 mi W of Clayton, Sunbeam Hot Springs, 316; Owhyee Co., 10 mi SE of Bruneau, Hot Creek Falls, 318, (near *P. brodiei*).

Washington, Chelan Co., Peshastin, river bank 1438, (glabrous phase).

*P. pacificum*,  $n = 9$

British Columbia, Kootenai District, Fairmont Hot Springs, 1189.

California, Del Norte Co., Gasquet, in open woods along road, 603; Shasta Co., Castle Crags, at old logging landing, 617; 1 mi W of Redding on Calif. Highway 299, creek bed, 2116; between head of Whiskeytown Lake and French Gulch along California Highway 299, creek bank, 2137.

Idaho, Elmore Co., Atlanta, bare warm dirt, 512; Idaho Co., 10 mi E of Lowell on banks of Lochsa River, 1489.

Montana, Lincoln Co., 3 mi NW of Troy on Kootenai River, 1498.

Oregon, Lane Co., Belknap Hot Springs, 1600.

Washington, Pierce Co., 4 mi S of Spanaway, open gravelly ground, 1499; along Interstate 5 at Steilacoom Exit, 2133; Snohomish Co., Sultan, borrow pit near river, 1526; 2 mi E of Gold Bar in sandy opening near river, 2131.

*P. tennesseense*,  $n = 9$

Ontario, Norfolk Co., Long Point Park, *J. S. Pringle, s.n.*

*P. thermale*,  $n = 9$

California, Lassen Volcanic National Park, Sulfur Works, mineralized soil, 472; Sonoma Co., The Geysers, 402, 1307.

Wyoming, Yellowstone National Park, Mammoth, 529; 5 mi N of Norris, edge of warm stream, 532; Roaring Mountain, 535.

---

## SYNTHETIC HYBRIDS

Synthetic hybrids were made by techniques described in Spellenberg (1975). Hybrids were easy to obtain in most combinations; more than 1100 individual cross pollinations were attempted in about 50 combinations. Data regarding hybrid seed set and hybrid seed germination (reported in Spellenberg, 1968) are not considered particularly relevant for ascertaining the degree of relationship between populations for several reasons: (1) because of the small size of the spikelets, damage to the gynoeceum often occurred when anthers were being removed from the opening floret prior to cross pollination; (2) the crossing process is tedious and often very few individual flowers were crossed, producing only a small sample of crossed florets; (3) plump, field-collected seed commonly have a low frequency of germination under greenhouse conditions, most seeds from some populations apparently requiring some unknown combination of factors prior to germination (Lelong, 1965; Spellenberg, 1968). These points in combination may account for the few crosses where no hybrids were obtained. The unsuccessful crosses were between populations that did not differ morphologically from one another more than those that produced successful crosses and are much more similar than *P. pacificum* and *P. scribnerianum* Nash between which successful crosses were made (Spellenberg, 1970). Thus the discussion regarding synthetic hybridization is restricted only to those crosses that produced  $F_1$  progeny.

In all but one of the crosses, progeny were vigorous, flowered normally the first summer after winter germination, and were intermediate between the parents in morphology and time of initial onset of flowering (if this differed in parents) under greenhouse conditions. One exception to this was the progeny from the cross *P. pacificum* (Ida., Atlanta, 512)  $\times$  *P. thermale* (Yellowstone, 532). (The seed parent is presented first in all crosses discussed; collection numbers are the author's). The 26 seedlings were very weak and difficult to establish; 14 were grown for nearly six months but all produced very small weak plants; the two most robust were kept for 2.5 years. None flowered but instead appeared much like diminutive, densely fasciated winter rosettes. Both parent plants used in this cross produced normal progeny when crossed with other populations.

Meiosis in hybrids was examined by standard techniques reported elsewhere (Spellenberg 1970; 1975). Parent plants consistently formed nine normal-appearing bivalents and in the  $F_1$  hybrids, where an attempt was made to examine at least 50–100 meiocytes, only 2–20 percent of the meiocytes exhibited abnormalities such as univalents, lagging chromosomes or fragments, anaphase bridges, and micronuclei or rarely microcytes. Higher frequencies of irregularities were noted in the progeny from a few crosses. Parents of *P. thermale* (Mt. Lassen Nat. Pk., 472) and *P. occidentale* (Ida., Owhyee Co., 318) carried large translocations

and in progeny from two crosses produced up to about 50 percent abnormal meioses (Spellenberg, 1975). In a cross involving *P. lanuginosum* (1862) and *P. pacificum* (2116), 40 percent of the metaphase I figures showed lagging chromosomes, but later stages were normal. No greater or lesser percentage of meiotic abnormality could be correlated with traditional taxonomic delimitation of western species, but rather a local population apparently may accumulate a number of chromosomal differences that appear in hybrid meioses. This is illustrated by three intraspecific crosses in *P. pacificum* (cf. fig. 2). In the cross 2137  $\times$  2116 (from California, 21 km apart), of 60 metaphase I meiocytes viewed, eight had a lagging univalent, but of 38 telophase I cells only two showed micronuclei. In 2133  $\times$  1231 (from Washington, 96 km apart), of 153 metaphase I meiocytes only one had a lagging chromosome. In 2137  $\times$  1189 (from California and British Columbia, 1280 km apart), of 65 cells viewed at diakinesis or metaphase I, no abnormalities were noted, and of 83 cell pairs at telophase I, all were normal.

Meiosis was examined in three of the trans-continental crosses (fig. 3). In *P. lanuginosum* (1862)  $\times$  *P. pacificum* (2116) diakinesis generally appeared normal, but of 30 metaphase I figures examined, 11 had single lagging chromosomes and three had two lagging chromosomes. However, in this cross the 35 telophase I pairs of cells examined appeared normal. In the cross *P. lanuginosum* (1862)  $\times$  *P. huachucae* (2185), of the 57 metaphase I meiocytes examined, only four had lagging univalents; few telophase I stages were seen, 11 were normal, and of the numerous telophase II cells scanned, about 2 percent had a small micronucleus. In the cross completing this triangle, *P. huachucae* (2158)  $\times$  *P. pacificum* (2116) all 49 metaphase I cells viewed appeared normal, and all 95 telophase I cell pairs examined were normal except for remnants of an anaphase I bridge in three. Meiosis in these crosses and all others examined indicate a high degree of homology among the genomes of these species.

Fertility of parent and hybrid plants was estimated by immediately staining pollen from mature undehisced or dehiscing anthers of living plants in a solution of lactophenol-cotton blue. Evenly swollen and stained grains were considered normal; blotchy and smaller ones or those that were shrunken and non-staining were considered non-viable. Pollen from parent plants was generally 85–100 percent evenly stained and rarely was smaller and unevenly stained as it commonly was in the hybrids. Percentages are based on samples of 200 grains. The results are illustrated in Figures 2 and 3; where more than one count was obtained, a range is given. In some individual hybrids the percentage of stainable pollen varied little from count to count; in others variation was relatively large. A few of the parent plants had a comparatively low frequency of evenly staining grains: *P. pacificum* (1189) (63–75%), *P. thermale* (402) (63–76%), *P. thermale* (472) (74–

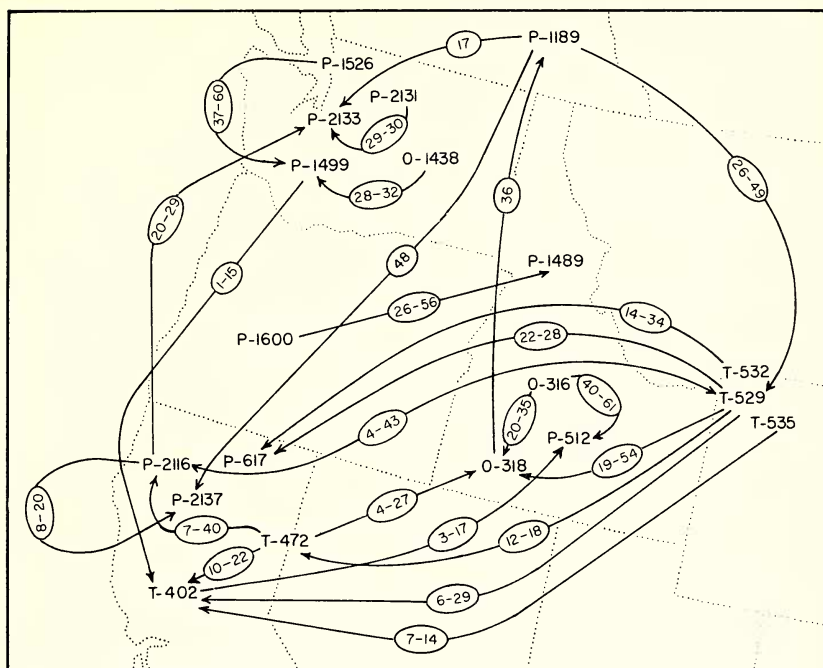


FIG. 2. Summary of synthetic hybridizations between western North American populations of *Dichanthelium lanuginosum*. P, O, and T preceding collection numbers refer to *Panicum pacificum*, *P. occidentale*, and *P. thermale* respectively. Arrows indicate cross, head of arrow points to seed parent, numbers in oval refer to percentage of stainable pollen in hybrid.

94%). In most instances in the hybrids, pollen viability is considerably less than would be estimated by abnormal meioses alone and the lower fertility must be attributed to genetic differences that are not observable at meiosis. There appears to be a weak tendency for hybrids to be of lower fertility as geographic distance between the parent populations increases, regardless of the plants involved in the cross, as long as crosses remain within the group *Lanuginosa* (cf. intergroup hybrids in Spellenberg, 1970), or are between closely related groups (*P. lindheimeri* in Figure 3 is in group *Spretia*). Interfertility between eastern and western species is not lower than between many western populations. It is also notable that all the *P. thermale* (sensu lato) populations when intercrossed show as low or lower fertility in hybrids than many interspecific western crosses, arguing, possibly, for independent origin or long separation of each of the *P. thermale* populations.

As Spellenberg (1975) demonstrated for progeny from a few crosses in these grasses followed to the  $F_3$  generation, fertility in some lines returns to normal (85–100%). These highly fertile progeny slightly differ morphologically from each of the parents. They may also be



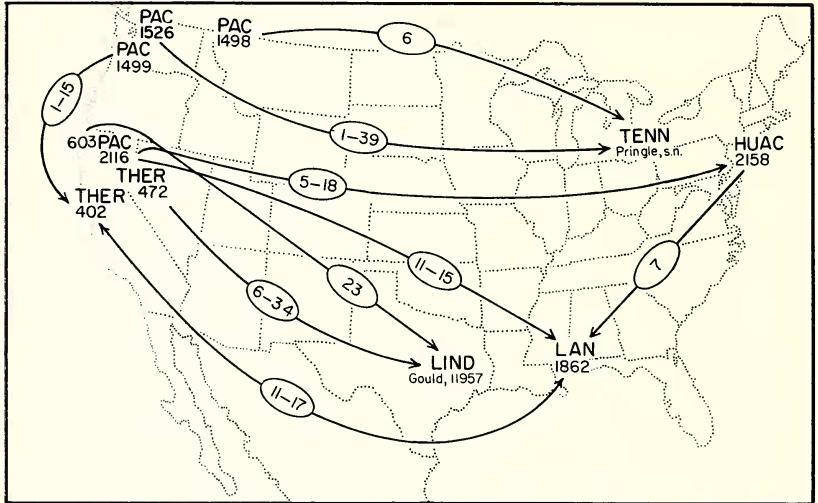


FIG. 3. Summary of transcontinental crosses in *Dichanthelium*, mostly group *Lanuginosa*. Under traditional treatment: HUAC = *Panicum huachucae*; LAN = *P. lanuginosum*; LIND = *P. lindheimeri* (in group *Spreta*); PAC = *P. pacificum*; TENN = *P. tennesseense*; THER = *P. thermale*. In revised treatment all except *P. lindheimeri* are included in *D. lanuginosum*. Arrows indicate cross, head of arrow points to seed parent, numbers in oval refer to percentage of stainable pollen in hybrid.

expected to be at least partially reproductively isolated from the parent plants due to recombination of factors promoting intersterility (Grant, 1958, pp. 355-357). The complex pattern of morphological variation seen in *Dichanthelium* probably is due in part to the coupling of a primarily autogamous system of reproduction with occasional hybridization and presents the expected taxonomic problems (Lewis, 1963). I am interpreting this complex as many highly inbred populations, most populations accumulating larger or smaller genetic differences, causing partial reproductive isolation between the populations. The most strongly isolated populations might be considered microspecies; few, however, are morphologically distinct. The overall variation seems minor, often even trivial, and to be about the same as that seen in many widely distributed xenogamous species. Following Lewis' (1963) suggestion for such groups, and following other authors' leads in floristic works for portions of the eastern United States, I am combining all the western forms under one name, *Dichanthelium lanuginosum* (Ell.) Gould.

#### TAXONOMY

The generic name *Dichanthelium* is adopted for the remainder of this paper. Of the few species of *Dichanthelium* in the western United States, *D. oligoanthes* (Schult.) Gould var. *scribnerianum* (Nash) Gould

(= *Panicum scribnerianum* Nash) (group *Oligosanthos*) is distinguished from the rest by having the largest spikelets (2.9–3.5 mm long), shortest ligules (0.5–1.5 mm long), and adaxial surfaces of the blades glabrous. Nearly or completely sterile hybrids between *D. lanuginosum* and *D. oligosanthos* occur rarely in the West. They bear spikelets 2.4–2.7 mm long, which have not been observed to perfect seed, and have ligules 1.0–3.0 mm long. Those from one area have been named *Panicum shastense* Scribn. & Merr. (Spellenberg, 1970). All these hybrids can be separated only with difficulty from *D. lanuginosum* var. *villosissimum* (Nash) Gould (= *P. villosissimum* Nash) collected once along the Columbia River near Troutdale, Oregon (Spellenberg, 1971). (My inclination is to recognize this variety as a species but to do so requires a new combination in *Dichanthelium*, which I would rather leave to one more experienced with this eastern form.) The single known specimen of this variety from the West has short dense hairs on the adaxial surfaces of the blades and is sparingly branched. All the remaining small-spikeleted (1.6–2.0 mm) western United States forms are included in this treatment except for the southern California record of *D. lindheimeri* (Nash) Gould (= *P. funstonii* Scribn. & Merr.). *Dichanthelium lindheimeri*, placed in the separate informal group *Spreta* in *Panicum* by Hitchcock and Chase (1910), is closely related to *D. lanuginosum* and the two can be easily crossed (fig. 3). Some authors of eastern United States botany (e.g., Gleason, 1952) maintain that the former is merely a variety of the latter, whereas others (e.g., Gould, 1975) maintain them as distinct species. Again I beg the issue, requiring a greater familiarity with the morass of intergrading eastern forms.

DICHANTHELIUM LANUGINOSUM (Ell.) Gould, *Brittonia* 26:60, 1974. — *P. lanuginosum* Ell., *Bot. S. C. and Ga.* 1:123, 1816. HOLOTYPE: *Dr. Baldwin*, "Hab. Georg.", CHARL!

Tufted perennials, subglabrous to densely pubescent throughout, overwintering as a more or less well marked rosette of usually short, broad leaves relatively stiff in nature as compared with the vernal and aestival foliage; culms at first simple, (5)15–65(80) cm tall and bearing lanceolate to linear-lanceolate blades and a terminal panicle; branch culms arising at the nodes of the vernal culms, sometimes attaining their height, but usually much shorter, branching repeatedly and forming loose to rather dense fascicles of reduced leaves and branches; nodes usually with a dense ring of more or less ascending to slightly reflexed hairs 0.5–1.0 mm long and with a glabrous ring below; sheaths of the vernal leaves (1.5)3–7(9) cm long, averaging about half the length of the internodes; ligule (actually a "pseudoligule" immediately above the minute true ligule) a dense ring of hairs (2.5)3–4(5) mm long; vernal blades lanceolate or linear-lanceolate, erect, ascending, or more or less spreading, (2.5)5–10(13) cm long, (3)5–10(15) mm wide, the upper-

most reduced, the margins usually with pustulate-based cilia at least at the base of the blade; panicles of the vernal culms generally well exerted, open and more or less ovate, (3)4–9(13) cm long and about as wide, the axis usually pubescent, the lower branches spreading, ascending, or occasionally somewhat reflexed, the upper ascending; panicles of the shorter branch culms usually less strongly exerted, reduced, the smallest usually more or less included in the fascicles of leaves; spikelets of the terminal primary panicles (1.5)1.6–2.0(2.1) mm long, about 0.8–1.1 mm wide, those of the branch panicles slightly smaller, more or less obovate-elliptic, subobtusate, pubescent with hairs about 0.1 mm long; first glume  $\frac{1}{4}$ – $\frac{1}{3}$  the length of the spikelet, usually with a faint nerve, or occasionally also with two smaller lateral nerves; the upper margin irregularly truncate to subacuminate; second glume and lemma equal, 7–9 nerved, slightly shorter than the fruit at maturity; sterile palea about half the length of the sterile lemma, hyaline, broadly ovate-lanceolate, notched at the tip to deeply divided; fertile lemma chartaceous-indurate, glossy, subacute and occasionally with a small rounded apiculus, its inrolled margins clasping a palea of similar texture, the two structures enclosing the caryopsis at maturity; fruit (including the lemma and palea) 1.5–1.7 mm long and about 0.9 mm wide;  $2n = 18$ . March through August.

Sandy lake margins or riverbanks, moist to rather dry prairies, open woods, or sometimes in marshy areas, common in disturbed ground, from sea level to about 1370 m, but ascending to 2280 m about hot springs in the western mountains, southern British Columbia to Nova Scotia, south to the Gulf States and southern California, extending into Mexico; introduced in Japan; sporadic in areas of low rainfall (western distribution; fig. 4).

This species is considered an assemblage of wholly intergradient forms previously recognized at the specific level on the basis of such features as density and distribution of pubescence, minute differences in spikelet length, and the nature of branching and habit of the culms. Pohl (1947), studying these grasses in the northeastern United States, placed all forms under *P. implicatum* Scribn., maintaining *P. lanuginosum* as a separate southeastern species, noting that the complex pattern of variation might not allow for the useful application of a subspecific category. In the treatment of the western species presented here, only the variants that combine morphological and ecological distinctness are recognized.

#### Key to the western varieties of *D. lanuginosum*

1. Culms usually less than 30 cm tall, stiffly ascending or spreading, in compact tufts; sheaths about  $\frac{1}{2}$  the length of the internodes or longer, often prominently papillose; blades generally less than 6 cm long, usually less than 8 times as long as broad, all except the very lowermost usually pubescent on the adaxial surface; about hot springs above 1370 m in the Rocky Mountains . . . 2. var. *sericeum*

1. Culms usually over 30 cm tall, ascending or spreading, often decumbent or sprawling, in loose bunches or dense tufts; sheaths usually about half the length of the internodes, the papillae generally not prominent; blades commonly longer than 6 cm, generally about 8 times their width or longer, from pubescent to glabrous on the adaxial surface.
2. Plants densely clothed with fine soft hairs; culms often densely branched above and reclining in the autumn phase; leaves strongly erect; primary panicle usually exerted from its sheath about the length of the panicle axis or less; leaves of winter rosette erect, with adaxial surfaces softly pubescent; plants from The Geysers, Sonoma Co., California . . . 3. var. *thermale*
2. Plants variously pubescent, glabrate, or glabrous on the adaxial surfaces of the blades or nearly throughout, but not finely and softly pubescent; culms usually erect or ascending in the autumnal phase, not often heavily branched above and reclining; leaves ascending or spreading, rarely erect; primary panicle generally exerted from the sheath well over the length of the panicle axis; leaves of winter rosette mostly ascending or spreading, the adaxial surface glabrous; widespread . . . 1. var. *fasciculatum*

1. **Dichanthelium lanuginosum** (Ell.) Gould var. **fasciculatum** (Torr.) Spellenberg, comb. nov. — *Panicum dichotomum* L. var. *fasciculatum* Torr., Fl. North and Mid. U.S. 145. 1824. — *P. huachucae* var. *fasciculatum* (Torr.) Hubb., Rhodora 14:171. 1912 — *P. lindheimeri* var. *fasciculatum* (Torr.) Fernald, Rhodora 23:288. 1921. — *P. lanuginosum* var. *fasciculatum* (Torr.) Fernald, Rhodora 36:77. 1934. HOLOTYPE: "in sandy fields, New Jersey", said to be in the Columbia University Herbarium, now housed at NY, could not be located. Photograph of type, US.

*Panicum dichotomum* var. *pubescens* Munro ex Benth., nom. nud. Pl. Hartw. 341. 1857. Sacramento, Calif., Hartweg 2024, fragment at US!

*Panicum huachucae* Ashe, J. Elisha Mitchell Sci. Soc. 15:51. 1898 — *P. lanuginosum* var. *huachucae* (Ashe) Hitchc., Rhodora 8:208. 1906. HOLOTYPE: Lemmon, in 1882, "Huachucae Mts. Ariz.", US!

*Panicum tennesseense* Ashe, J. Elisha Mitchell Sci. Soc. 15:52. 1898. — *Panicum lanuginosum* var. *tennesseense* (Ashe) Gleason, Phytologia 4:21. 1952. HOLOTYPE: No. 7087 Biltmore Herbarium; Cedar Glades, La Vergne Co., Tennessee, 7 Aug 1897, not located; fragments and photograph of type at US!

*Panicum occidentale* Scribn., Annual Rep. Missouri Bot. Gard. 10:48. 1899. HOLOTYPE: Haenke, the locality as published by Presl in Reliquiae Haenkeanae "Hab. in Nootka-Sund", Vancouver Island,

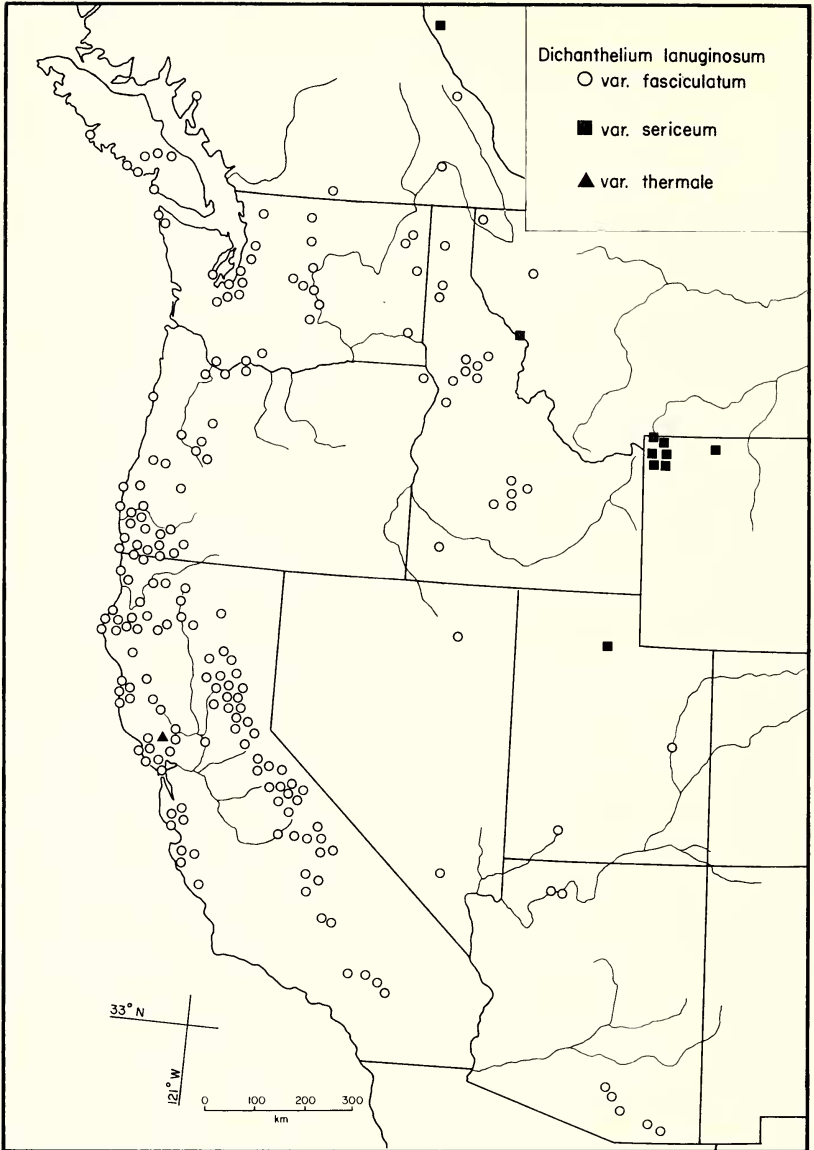


FIG. 4. Distribution of the varieties of *Dichanthelium lanuginosum* in western North America.

British Columbia, PR; photograph and fragments at US. ISO-TYPE: The specimen Scribner saw when he named the species, but did not formally describe it, is believed to be in the Bernhardt Herbarium at MO; not located. PARATYPE: A. A. & E. G. Heller 3978, "collected near Montesano, Chehalis Co., Wash.", US! UC!

*Panicum huachucae* var. *silvicola* Hitchc. & Chase in Robinson, Rhodora 10:64. 1908. HOLOTYPE: *A. Chase 2400*, "Woods border, Reno, District of Columbia", US!

*Panicum pacificum* Hitchc. & Chase, Contr. U. S. Natl. Herb. 15:299. 1910. HOLOTYPE: *A. S. Hitchcock 3070*, Amer. Gr. Nat. Herb. no. 136, "in moist places in woods", Castle Crags, Shasta Co., Calif., US! ISOTYPES: CAS! UC! WTU!

*Panicum brodiei* St. John, Fl. Southeast. Wash. and Adj. Idaho, 51. 1937. HOLOTYPE: *D. A. Brodie*, Wawai, Snake River, Whitman Co., Wash., June 1893, WS! photograph UC!

*Panicum lassenianum* Schmolz, Madroño 5:95. 1939. HOLOTYPE: *W. L. Jepson 4082*, Devil's Kitchen, Hot Spring Valley, Plumas Co., Calif., US.

Diagnostic features: Leaves of winter rosette usually glabrous on the adaxial, and sometimes on the abaxial, surface; culms (5)30–60(80) cm tall, the autumnal form with branches short and tightly fascicled at the summit of the sheath or with longer and more loosely fascicled branches; sheaths of vernal leaves (2)3–6(8) cm long, about half the length of the internode; larger vernal blades linear-lanceolate to lanceolate (2.5)5–10(12) cm long, averaging more than 8.2 times as long as broad, pubescent, glabrate, or glabrous on the adaxial surface; primary panicles (3)4–9(13) cm long and about as wide; spikelets of the terminal panicles (1.5)1.6–2.0(2.1) mm long (averaging 1.65 mm east of the Rocky Mts., 1.8 mm westward);  $2n = 18$ . March through August.

Sandy lake margins, riverbanks, coastal slopes, marshy areas, moist to rather dry prairies from sea level to about 1370 m in Idaho and to 2120 m in the Sierra Nevada, southern British Columbia to Nova Scotia southward to southern California and the Gulf States; introduced in Japan (western distribution, fig. 4).

*Dichanthelium lanuginosum* var. *fasciculatum* is a widespread, variable assemblage of forms that includes no clearly separable entities. If the plants were generally pubescent they generally have been placed previously in *Panicum huachucae* when collected from Arizona eastward, or in *P. pacificum* if collected from California to British Columbia and Montana. Hitchcock and Chase stated that these two taxa resemble one another, but maintained that the spreading habit of *P. pacificum*, its larger spikelets, and its distinct range made it impossible to include it with the other. The spikelets of *P. huachucae* are 1.6–1.8 mm long, whereas those of *P. pacificum* are said to be 1.8–2.0 mm long, but numerous collections have spikelets shorter than this (fig. 1). *Panicum pacificum* is also said to have decumbent or prostrate-spreading autumnal culms, those of *P. huachucae* being stiffly erect or ascending. Most specimens of *P. pacificum* are collected too early in the season to indicate their autumnal form, but among those collected late in the season erect-

ascending forms are common. Most of my living collections have also had erect-ascending culms in the fall.

I have also included *P. lassenianum*, usually placed in *P. thermale*, in this variety. In describing the species, Schmoll (1939) noted its resemblance to *P. pacificum* of the Sierran region, although plants from the Mt. Lassen region tend to have slightly shorter leaves. Spikelets of the two are about the same length. Schmoll indicates the difficulty of separating the two by annotating as "*P. pacificum*-group?" the collection *J. Swallen 878* ("moist soil along creek close to hot sulphur springs. Trail to Lassen Peak", US). Such specimens as this and those of *T. H. Kearney*, Boiling Springs Lake, near Drakesbad, CAS; *J. T. Howell 35771*, Boiling Spring Lake, CAS; *H. N. Bolander 2169*, hot spring, southeast of Lassen's Peak, US; *R. Spellenberg 1229d*, Devil's Kitchen, WTU—all from the vicinity of Mt. Lassen, Calif.—are inseparable from more or less short, broad-leaved forms of *P. pacificum*, especially those from higher elevations in the Sierra Nevada. *Panicum lassenianum* is near the northern limit of these grasses in these mountains and may be part of a physiologically differentiated climatic and edaphic ecotype. However, I believe it is insufficiently distinct to be given formal taxonomic recognition.

When compared to var. *thermale* from The Geysers, the plants from the vicinity of Mt. Lassen are shorter (average culm length is 22 cm versus 40 cm), have shorter vernal blades, and have low winter rosettes of short, broad, more or less glabrous leaves. Though plants from these two areas are readily separable, those from Lassen are much more difficult to distinguish from some of those of var. *sericeum* from Yellowstone. Plants from the Lassen region have spikelets averaging 1.9 mm in length, 0.2 mm greater than the average of those of the var. *sericeum*, but spikelet lengths of plants of Lassen and Yellowstone completely intergrade. The leaves of the Lassen plants are slightly longer on the average but are not clearly different from those of the var. *sericeum*. Although the proportions of the leaves from the two populations overlap, the length/width ratio of those from Lassen averages about 8.4, whereas that of var. *sericeum* averages 6.5. As Schmoll noted, the abaxial blade surfaces of the Lassen plants are less densely pubescent than those of var. *sericeum* but this distinction is so subtle that it is of little diagnostic value.

Included in variety *fasciculatum* is *P. occidentale*, the western form with glabrate or glabrous adaxial surfaces of the blades. I earlier annotated such specimens as *P. lanuginosum* var. *tennesseense*, but such a separation is arbitrary and has no ecological, morphological, or geographic significance. The following collections are mixed, containing forms formerly referred to *P. pacificum* and *P. occidentale*:

*J. B. Davy 5894*, "among rocks, Martin's Ferry," Humboldt Co., Calif. (UC); *J. B. Davy and W. C. Blasedale 5971*, Crescent City, Del Norte Co., Calif. (UC 53350 = "*P. pacificum*", UC 39267 = "*P. occidentale*"),

*J. T. Howell 381*, along Merced River, Wawona, Mariposa Co., Calif., CAS; *P. H. Raven 4885*, hot springs, Blaney Meadows, Fresno Co., Calif., UC; *J. P. Tracy 5014*, boggy ground, White Thorn Valley, Humboldt Co., Calif., UC; *J. P. Tracy 9427*, along river, Trinity River Valley, at Willow Creek, Humboldt Co., Calif. (CAS = *P. occidentale*", UC = *P. pacificum*"').

A number of collections have such short hairs or are so sparsely pubescent on the adaxial blade surfaces that they can be considered intermediate between forms formerly referred to *P. pacificum* and *P. occidentale*. A few of these are:

*B. Bolt 503*, Big Trees quadrangle, Tuolumne Co., Calif., UC; *J. B. Davy 6745*, Point Reyes Peninsula, Marin Co., Calif., UC; *A. Eastwood and J. T. Howell 3613*, Craft Lake, Coos Co., Ore., CAS; *J. A. Ewan 10482*, 5 mi S of Bandon, Coos Co., Ore., WTU; *J. B. Flett*, in 1897, prairie, Tacoma, Wash., WTU; *A. E. and E. G. Heller 3978*, near Montesano, Chehalis Co., Wash., UC; *F. L. Henderson*, in 1892, prairies of Pierce and Thurston Co's., Wash., WTU; *R. F. Hoover 2418*, Ione, Amador Co., Calif., UC; *R. F. Hoover 5140*, 5 mi NW of Santa Cruz on Empire Grade Rd., Santa Cruz Co., Calif., UC; *J. T. Howell 29842*, 1.5 mi NNE of Buena Vista, Amador Co., Calif., CAS.

Plants from about Point Reyes, California, to Nootka Sound, Vancouver Island, British Columbia, form a more or less recognizable coastal race distinguished by their tendency to be tightly tufted, the branch culms attaining about half the height of the vernal culms, the plants thus appearing leafy below. A plant with glabrous adaxial surfaces of the blades from this race was described as *P. occidentale*. In the interior, plants are commonly taller and more open and seemingly less leafy below. A robust plant of this form was described as *P. brodiei*. It is through these forms of the interior that typical *P. occidentale* grades into *P. tennesseense*, but some plants of the latter, especially in the Great Lakes region, have habits similar to that of the coastal race of the West.

*Dichanthelium lanuginosum* var. *fasciculatum* also intergrades with the southeastern var. *lanuginosum* through such lightly pubescent material as *S. M. Tracy 4508* (Biloxi, Miss., NY!, US, the type collection of *P. ciliosum*, a synonym of *P. lanuginosum*, sensu stricto) or such short-spikeleted, generally pubescent plants as *D. J. Banks 201* (roadside 1 mi SE of Boaz, Marshall Co., Ala., US) or *G. V. Nash* (vicinity of Lake Eustice, Lake Co., Fla., April 1-15, 1894, US). Numerous collections from eastern Texas are also intermediate between the two.

In two areas of the Northwest (including north coastal California where *P. occidentale* and *P. pacificum* are sympatric) plants that are subglabrous or glabrous are fairly common. These plants approach *P. lindheimeri*, a species distinguished by its elongate internodes, glabrous leaves and wiry culms, and small spikelets averaging about 1.5 mm long, widespread in the eastern half of the country but occurring sporadically



through the Southwest and into southern California as *P. funstonii* (*F. W. Coville and F. Funston 1286*, "on the banks of the Kaweah River, at Three Rivers, Tulare Co., Calif.", US!). Most of the plants from the Northwest that approach this species are more compact, have sparsely pubescent or puberulent sheaths, culms, or abaxial blade surfaces, and may in some have spikelets over 1.7 mm long. Since I am not very familiar with the *Spreta* group in the field, or the relationship between this group and the group *Lanuginosa*, I am hesitant to place these forms into *D. lindheimeri*, extending the range of that species 1600 km, or to place *D. lindheimeri* into *D. lanuginosum* as a variety, as Gleason (1952) and Fernald (1934) have done. Instead, I consider these plants to be representative of one of the extremes of variation in *D. lanuginosum* in the West. They are:

*A. S. Hitchcock*, Amer. Gr. Nat. Herb. no. 527, Eureka, Calif., UC; *A. R. Kruckeberg 2320*, Imnaha River, Wallowa Co., Ore., WTU, ORE, UC, OSC; *R. Spellenberg 1436*, Peshastin, and *1532*, Leavenworth, Chelan Co., Wash., WTU; *W. N. Suksdorf 5162*, and *5174*, Bingen, Klickitat Co., Wash., UC; *J. P. Tracy 925*, in wet ground at Eureka, Humboldt Co., Calif., (a mixed collection of glabrous and more or less pubescent plants), CAS; *J. P. Tracy 4645*, at Eureka, Humboldt Co., Calif., (a collection on which Tracy has noted "least pilose form" and is similar, except in pubescence, to his collection *4644*, on which he has noted "moderately pilose form") both at UC; *K. Whited*, in 1901, Tumwater Canyon, Chelan Co., Wash., WTU.

2. ***Dichanthelium lanuginosum* var. *sericeum*** (Schmoll) Spellenberg, comb. nov. — *Panicum ferventicola* var. *sericeum* Schmoll, Madroño 5:92. 1939. HOLOTYPE: *A. Nelson 6037*, Mammoth Hot Springs, Yellowstone National Park, Wyoming, RM. ISOTYPES: G, US!

*Panicum ferventicola* Schmoll, Madroño 5:92. 1939. HOLOTYPE: *A. Chase*, Amer. Gr. Natl. Herb. no. 137, 5 mi N of Norris Geyser Basin, Yellowstone National Park, Wyoming, G. ISOTYPES: UC! US! PARATYPES: *E. A. Mearns 4203*, "The Thumb, Yellowstone Lake", US! *A. S. Hitchcock 1902*, Norris Basin, around hot springs", US!

*Panicum ferventicola* var. *papillosum* Schmoll, Madroño 5:94. 1939. HOLOTYPE: *A. S. Hitchcock*, Amer. Gr. Natl. Herb. no. 220, Banff, Alberta, G. ISOTYPES: F, UC!

Diagnostic features: Plants low, tufted, densely pubescent (rarely subglabrous), sometimes forming dense mats; vernal culms (5)7–28(35) cm tall, stiffly erect-ascending to more or less spreading; branch culms attaining about half the height of the vernal culms, the plants thus appearing densely leafy below; sheaths often equaling or exceeding the

internodes, averaging 0.8–0.9 times their length, densely villous with ascending or spreading, often prominently papillate-based hairs; vernal blades ascending or spreading, rarely erect, (3)4–6(7.5) mm long, (5)6–10(14) mm wide, the length/width ratio averaging 6.5, the upper surface moderately to densely pubescent, rarely glabrous; primary panicles usually well exerted, (2.5)3–7(8) cm long and about as broad; spikelets (1.5)1.6–1.8(1.9) mm long;  $2n = 18$ . Mid-June through August.

About geysers, hot springs, and fumaroles, in gravelly, mineralized soil to heavy soil along warm creeks, usually in warm or hot ground, in the Rocky Mountains from about 1370 m at Banff, where probably extinct due to commercial development, south to Yellowstone National Park where it occurs at up to 2280 m, east to Buffalo Fork, Bighorn Co., Wyoming; reported from one collection from a garden in Salt Lake City, Utah (*W. A. Stanton, 826, US*) (fig. 4).

Variety *sericeum* is distinguished from the other varieties by its short culms, tightly clumped habit, and short, broad leaves. This tendency toward relatively broad leaves reaches its extreme in plants from Banff where the blade length is only about four times that of the width. The average length/width ratio rarely exceeds 8.0, serving to separate it from most of the plants of var. *fasciculatum* from nearby areas. Some plants from Lolo Hot Springs, Missoula Co., Montana, are low, tufted, and broad-leaved (*W. Griffiths 306, US*) and are readily placed in the var. *sericeum*, whereas others from the same springs (*R. Spellenberg 545, WTU*) have elongated culms and leaves slightly longer than 8.0 times their width, thus more closely resembling var. *fasciculatum*.

Other collections that on the basis of leaf proportions approach northern forms of *D. lanuginosum* var. *fasciculatum* are:

*E. C. S. 319*, Mammoth Hot Springs, US; *A. S. Hitchcock 2061*, Washburn Hot Springs, US; *A. S. Hitchcock 2086*, hot springs, 1 mi north of Thumb, US; *J. W. Lettermann*, in 1885, Hayden's Valley, US; all from Yellowstone, and *R. Spellenberg 523*, Huckleberry Hot Springs, Teton Co., Wyo., WTU.

3. *Dichanthelium lanuginosum* var. *thermale* (Bolander.) Spellenberg stat. et comb. nov. — *Panicum thermale* Bolander., Proc. Calif. Acad. Sci. 2:181. 1862. HOLOTYPE: *H. N. Bolander 3941*, The Geysers, Sonoma Co., Calif., G. ISOTYPES: US! UC! CAS!

Diagnostic features: Plants forming large tufts, (30)35–50(60) cm tall, densely and softly pubescent throughout, or occasionally only sparsely pubescent on the abaxial surfaces of the blades; winter rosette of erect culms and leaves  $\frac{1}{5}$ – $\frac{1}{4}$  the height of the vernal culms, densely pubescent; sheaths (2.5)3–4(5) cm long, averaging about half the length of the internodes; vernal blades erect, (7)8–11(13) cm long, (5)6–8(10) mm wide, the blade length/width ratio usually over 10 and averaging 13.6, panicles usually exerted from the sheath only about the length of the

panicle axis or less, (4)5–9(11) cm long, about as wide; spikelets (1.7)1.8–2.0(2.1) mm long, averaging 1.9 mm:  $2n = 18$ . April to mid-August.

In mineralized, usually moist, warm "soil", at The Geysers, Sonoma Co., Calif. (fig. 4). The long standing record for Napa Co., based on *Brewer 861* (US), is probably in error. This specimen has two labels: one reads "At McDonald's Napa County" and the other reads "growing around all the Geysers Napa Co.". Correspondence with the Sonoma County Records Office has disclosed that a McDonald owned the property around The Geysers, Sonoma Co., in 1897, and probably before. I have seen no collections of *Dichanthelium* from hot springs in Napa Co.

This variety includes one of the most distinct forms of *Dichanthelium* from the West. Variety *thermale* is outwardly most similar to plants of var. *lanuginosum* from the Gulf Coastal Plain. They have similar habits late in season, the form of the fascicled branches of the two is sometimes similar, and both are densely and softly pubescent. In general, var. *thermale* has leaves longer relative to their width (length/width ratio averaging 13.6), slightly larger spikelets, less spreading leaves on the branch culms, and no cilia on the margins in the upper half of the leaves of the aestival foliage. The few collections of var. *fasciculatum* from Sonoma and Napa counties somewhat resemble var. *thermale* especially in leaf habit and leaf proportions: *J. T. Howell 13032*, Pitkin Marsh, Sonoma Co., Calif. (CAS) and *J. T. Howell 18240*, hills SW of St. Helena, Napa Co., Calif. (CAS).

#### ACKNOWLEDGMENTS

The bulk of this paper is based on a thesis submitted to the University of Washington in partial fulfillment of the requirements for the Ph.D. degree. The guidance of Dr. C. L. Hitchcock and Dr. A. R. Kruckeberg is gratefully acknowledged. Gratitude is expressed to the curators of the various herbaria cited for making needed material available. Assistance from my wife in virtually all aspects of this work is deeply appreciated.

#### LITERATURE CITED

- CLARK, C. A. and F. W. GOULD. In press. Some epidermal characteristics of paleas of *Dichanthelium*, *Panicum*, and *Echinochloa*. *Amer. J. Bot.*
- FERNALD, M. L. 1921. The Gray Herbarium expedition to Nova Scotia, (cont.). *Rhodora* 23:233–245.
- . 1934. Realignment in the genus *Panicum*. *Rhodora* 36:61–87.
- GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the north-eastern United States and adjacent Canada. Lancaster Press, Inc., Lancaster.
- GOULD, F. W. 1974. Nomenclatural changes in the Poaceae. *Brittonia* 26:59–60.
- GRANT, V. 1958. The regulation of recombination in plants. Cold Spring Harbor Symp. Quant. Biol. 23:337–363.
- HITCHCOCK, A. S. 1951. Manual of the grasses of the United States. Ed. 2 revised by Agnes Chase. U. S. Dept. Agric. Misc. Publ. 200.
- and A. Chase. 1910. The North American species of *Panicum*. *Contr. U. S. Natl. Herb.* 15:1–396.

- JEPSON, W. L. 1911. A flora of western middle California, ed. 2. Cunningham, Curtiss & Welch, San Francisco.
- LELONG, M. G. 1965. Studies in the reproduction and variation in some *Panicum* subgenus *Dichanthelium*. Thesis: Ph.D., Iowa State Univ., Ames (Univ. Microfilms, Ann Arbor, Michigan; Diss. Abstr. 26:4993).
- LEWIS, H. 1963. The taxonomic problem of inbreeders or how to solve any taxonomic problem. *Regnum Veg.* 27:37-44.
- MAYR, E. 1969. Principles of systematic zoology. McGraw-Hill, Inc., N. Y.
- POHL, R. W. 1947. A taxonomic study on the grasses of Pennsylvania. *Amer. Midl. Naturalist* 38:513-604.
- SCHMOLL, H. M. 1939. A realignment of the *Panicum thermale* group. *Madroño* 5:90-96.
- SHINNERS, L. H. 1944. Notes on Wisconsin grasses. IV. *Leptoloma* and *Panicum*. *Amer. Midl. Naturalist* 32:164-180.
- SPELLENBERG, R. W. 1968. Biosystematic studies in *Panicum*, group Lanuginosa, from the Pacific Northwest. Thesis: Ph.D., Univ. Washington, Seattle (Univ. Microfilms, Ann Arbor, Michigan; Diss. Abstr. 68:7080).
- 1969. "*Panicum occidentale*", p. 637-638, In C. L. Hitchcock, A. Cronquist, and M. Ownbey, Vascular plants of the Pacific Northwest, Part 1. Univ. Wash. Press, Seattle.
- 1970. *Panicum shastense* (Gramineae), a sterile hybrid between *P. pacificum* and *P. scribnerianum*. *Brittonia* 22:154-162.
- 1971. Two species of *Panicum* (Poaceae) new to Oregon. *Madroño* 21:102-103.
- 1975. Autogamy and hybridization as evolutionary mechanisms in *Panicum*, subgenus *Dichanthelium* (Gramineae). *Brittonia* 27:87-95.
- VASEY, G. 1885. A descriptive catalogue of the grasses of the United States. Gibson, Washington, DC.
- WATSON, S. 1880. Botany, Vol. II (Geological Survey of Calif.). John Wilson & Son, Univ. Press, Cambridge, Mass.

## RELATIONSHIPS OF HESPEROLINON AND LINUM (LINACEAE)

C. M. ROGERS

Department of Biology, Wayne State University,  
Detroit, Michigan 48202

*Hesperolinon* is a genus of about a dozen closely related annuals, restricted mainly to serpentine soils of the North and South Coast Ranges of California. It was at first treated as a section of *Linum* (Gray, 1865) and later elevated to a genus (Small, 1907), a status upheld by Sharsmith (1961) who described *Hesperolinon* in some detail. At the same time, it is clearly related to *Linum* and its narrow geographical and ecological range, little morphological diversity, and rather high degree of specialization when compared to the large, diverse, and worldwide *Linum* suggest that *Hesperolinon* may be an evolutionary segregate of that genus.